THE HEAD OF AN EMBRYO AMPHIUMA.

By J. S. Kingsley.

The following is a preliminary account of some studies of a single stage of *Amphiuma means* before hatching. For the material I am under great obligations to Prof. O. P. Hay, of Irvington, Indiana. I must also return my thanks to Prof. Dr. Robert Wiedersheim, in whose private laboratory in the University of Freiburg i-B., my studies were conducted. Only one who has enjoyed the privilege of working with him can appreciate his many kindnesses and extreme helpfulness.

External appearance.—The general appearance of the eggs has already been described by Dr. Hay, and is strikingly similar to that of Ichthyophis as described and illustrated by the cousins Sarasin. This resemblance is strengthened by the fact that the cord connecting the eggs is spirally twisted as in the Ceylonese Gymnophione described by them.

The external description of the embryo Amphiuma has been correctly described by Hay in most points, but in a few respects my specimens differ from his description. According to him "the gills consist of three pairs, and are of the simply pinnate form. . . Only once have I observed any of these lateral filaments to divide. . . Three gill slits are still open." The figures which illustrate this are strikingly like those of the Sarasins of the branchiæ of the Ichthyophis larvæ. In the larvæ which I studied the resemblance is not so striking. The three gills of either side are united at the base into a common trunk, the gill filaments are not bipinnately but irregularly arranged, and in none of my specimens have I found more than one gill cleft open. (*Cf. infra.*)

Chondrocranium.—The cartilaginous skull, as it appears in a wax reconstruction after Born's method (and compared with dissections), is more slender than in Hay's figures; it also presents minor differences in several other respects from his rep-

resentation and description, to which reference should be made in reading the following account:

In front of the pituitary space the trabeculæ unite into a broad horizontal plate, the line of junction of the two halves being entirely obsolete, while still farther forward the cornua trabeculæ, instead of being two-lobed, form a broad triangular plate. Between the two cornua is a deep and narrow notch with parallel sides in which is imbedded the septum osseum of the premaxilla to be described below. The trabeculæ, on either side of the pituitary space, are high and compressed. Just behind the nasal capsules two processes are given off on either side. The upper one, arising from the trabecular crest is, as Hay calls it, the rudimentary nasal capsule, and in one specimen upon one side I found a perforation in this process which suggests the more extensive fenestration in the nasal cartilage of the adult Necturus and Protopterus. The lower process may retain the name, antorbital, usually applied to it, for Amphiuma presents no evidence that it is the palatine cartilage as Gaupp interprets it.

Somewhat farther behind these processes than in Hay's figure are two openings through the trabeculæ for the passage of the optic and oculomotorius[1] nerves.

The trabeculæ are united to the posterior portion of the cartilaginous skull by three processes. The upper connects the crista trabeculæ with the ear capsule; the middle, the process ascendens of Stöhr and other authors, goes from the trabeculæ to the inner anterior angle of the quadrate; the third, the radix trabeculæ, is bifurcate posteriorly, the outer ramus joining the floor of the otic capsule, the other uniting with the parachordal floor of the cranial cavity.

The parachordal cartilage lies beneath the notochord, as do the lower arcs of the occipital and first cervical vertebræ. Between the parachordals and the otic capsule on either side is a large oval opening in the cranial floor. The occipital vertebra is confluent below with the parachordal cartilage; on

[1]Hay suspected that the posterior of these foramina was for the transmission of the third nerve. I have traced the nerve from its origin, through the opening, into the proper eye muscles.

either side it merges with the posterior angle of the otic capsules; above it is incomplete. Between the ventral portion of the occipital vertebræ and its lateral union with the otic capsule is the foramen for the vagus nerve.

The otic capsules are elongate oval. In front they project slightly beyond the point of union with the cristæ trabecularum, behind they merge into the occipital vertebra. In the lower outer surface is the large oval foramen ovale, and just in front of it is the external opening of the foramen for the facialis. This foramen does not penetrate the ear capsule proper, it only passes through its anterior wall. On the inner lower surface the otic capsule is produced into a narrow ledge which projects inwards to form a part of the floor of the cranial cavity, being limited internally by the large opening between it and the parachordal cartilage. The inner wall of the capsule is perforated by three subequal openings in the same plane, and a fourth smaller one above them and between the two posterior ones. The anterior of these forms a considerable cavity, in which is situated the acustico-facialis ganglion and from it nerves go through the adjacent cartilage in the following directions: One branch, the ramus palatinus, goes ventrally through the floor; a second, the facialis proper, goes straight outward to reappear, as just mentioned, upon the outer surface; while the third, the ramus vestibularis of the eighth nerve, goes upward and backward to the sensory epithelium of the inner ear. Separated by a considerable cartilaginous interval from the first of these openings is a second, nearly equal in size, through which the ramus cochlearis of the auditory nerve enters the ear; the small upper opening permits the ductus endolymphaticus to pass above the brain in the same manner that the ductus perilymphaticus goes through the fourth opening beneath the brain. I have seen no special opening in the cartilage for the passage of blood-vessels to the inner ear.

Cartilaginous Visceral Skeleton.—The quadrate is rhomboidal in outline when viewed from the side, the external surface exhibiting a slight depression. As yet it is connected with the skull by only the process ascendens, the processes

oticus and palatobasale being as yet undeveloped. Behind, from the posterior angle, is a projection with which articulates the cylindrical process opercularis (columella), the posterior end of which is imbedded in the still membranous opercular membrane (stapes of Hay), which closes the foramen ovale. Meckel's cartilage articulates with the lower angle of the quadrate, a process extending behind the articulation, for the insertion of the digastric muscle. The two halves of the lower jaw are united by fibrous connective tissue in front. I find no trace of Hay's pterygoid cartilage. The hyoid and branchial arches call for no remark aside from the fact that they lack the yoke which binds together the upper ends of the branchial bars in Amblystoma embryos, and, according to Stöhr, in some other forms.

Ossifications.—These have been well described by Hay and only a few words are necessary. The ossifications are here, as Weidersheim has pointed out for all urodeles, perichondrostoses. They consist of, in the cranium at this stage, premaxillary, vomeropalatines (better dermopalatines), parasphenoid, frontals, parietals, squamosals or tympanics, occipital and small patches surrounding the exits of the vagus nerves. In the lower jaw dentary and angular bones are seen, while ossification occurs on the hyoids. The premaxillary at this comparatively early stage shows no trace of a double origin, either in front or in that median osseous process extending backwards, which separates the two nasal cavities. This is the septum osseum of Weidersheim, and is clearly a portion of the premaxillary. It is also, I think, the same bone which Cope has called ethmoid, and upon which both he and the Sarasins have placed great weight in their association of the Gymnophiona with the Amphiumidæ. The squamosal of Amphiuma is clearly not homologous with that bone which Weidersheim (and following him Cope) has called by that name in the Cæcilians, but to which the Sarasins have applied the name jugal. The ossification of the occipital region is peculiar. As is well known the occipital region of the urodele skull is formed by the junction of a primitively separate vertebra with the parachordals and otic capsules. In this vertebra, above its carti-

laginous lower arch and in the fibrous connective tissue on either side of the notochord is a deposit of bone of such a character as to suggest the existence here of an earlier vertebral centre which has disappeared.

VISCERAL CLEFTS.—My specimens are too old to throw any light upon the mooted question of an obsolete visceral segment between mandible and hyoid, but in the region behind the last branchial cleft of the ordinary Amphibian some interesting facts are seen. A reconstruction of the floor of the throat after the method of Born shows the following clefts distinctly: —*a*, the hyomandibular or spiracular cleft, which like *b* and *c*, the first and second branchials, is not open to the exterior; *d*, the third branchial cleft which is still functional, opening to the outer world as already described in referring to the external appearance. Behind this last cleft comes the fourth cartilaginous gill arch; and still behind this and between it and the trachea are two other pits, clearly serially homologous with the others, and hence to be regarded as the representatives of the two posterior clefts of the typical elasmobranchs and ganoids. Of these the anterior (fourth branchial) has already been recognized as occurring in the Amphibian ontogeny; it is the "Suprapericardialkörper" of authors, which Maurer has shown to be the fourth gill cleft. The posterior, the fifth gill cleft has not before been recognized in the Batrachia. These posterior clefts bear such relationships to the trachea as to lend countenance to that view which would derive lungs and trachea from modified gill slits. Should this view ever be substantiated, it may be that the laryngeal cartilages will be shown to be the modified gill-bars of this region. Amphiuma, however, throws not the slightest light directly upon the phylogeny of these structures.

In this connection I may state that in the early Siredon stage of *Amblystoma jeffersonianum* the posterior (fourth) branchial cartilage is bifid at its upper and posterior extremity[2] in such a manner as to suggest that there was formerly here an additional arch, the traces of which are disappearing in the same way in which the posterior gill of Ichthyophis is

[2] This, of course, bears no relationship to the bifid ceratohyals of the ganoids.

merged with its predecessor. In Amphiuma I find no trace of any gill bar behind the fourth of the adult.

NERVOUS SYSTEM.—The brain of the larva studied varies considerably from that of the adult as described by Osborn. The account of the internal structure is reserved until later. Externally it is characterized by its shortness and longitudinal compression, this being more marked than in any adult Batrachian except that of the Gymnophiona as described by Waldschmidt and Burckhardt. It exceeds in this respect the brain of Protopterus as figured by Fulliquet. As in the latter form the cerebral hemispheres are pushed back upon and wedged apart by the twixt brain, while behind, the mid-brain and cerebellum are so folded over upon the medulla that the lateral angles of the 'fossa rhomboidalis' extend nearly to the posterior lobes of the cerebrum.[3] The brain flexure, however, is apparently slight, the primary bend being corrected by a secondary one. The cerebral hemispheres are distinct above and in front of the lamina terminalis; the olfactory lobes are not distinct from the hemispheres. The floor of the twixt brain is very short and the infundibulum and hypophysis are very broad, the latter being wider than the mid-brain in its widest place. The choroid plexus of the anterior ventricles is well developed, but calls for no special remark. The cavity of the pinealis is still in connection with the cavity of the brain and its enlarged distal portion, which reaches nearly to the roof of the cranial cavity, is considerably lobed and folded.

The olfactory nerve arises by a single root,[4] goes laterally from the tip of the hemisphere and, in the nasal capsule, divides into upper and lower branches which innervate the nasal epithelium and Jacobson's organ respectively.

The optic and oculomotor nerves call for no comment. I failed to find the fourth (trochlearis) and the sixth (abducens) in my preparations.

The fifth nerve presents several features of interest. As my

[3]Cf. Waldschmidt's account of the Gymnophionan brain.

[4]Weidersheim formerly thought that the double origin of the olfactory in the Gymnophiona had great morphological importance, but the studies of the Sarasins and of Burckhardt show that such is not the case.

material was none too well preserved, I am not able to say how many roots the nerve has, as it comes from the brain. Several distinct groups of fibres go from the anterior angle of the medulla to the gasserian ganglion. This latter structure is single and shows none of the double character described by von Plessin and Rabinowicz[5] in *Salamandra maculata.* Nor do my studies of the nerve fibres agree with their accounts of the nerves. The Gasserian ganglion is oval in shape. It lies in the angle formed by the otic capsule, the processes of the trabeculæ and the process ascendens of the quadrate. From its hinder surface a commissure connects it with the ganglion acustico-facialis. From its outer surface arises the maxillaris inferior, and from its anterior end, at different levels, the rami ophthalmicus superficialis, ophthalmicus profundus and maxillaris superior. The maxillaris inferior and the maxillaris superior, after leaving the ganglion, pass from the cranial cavity between the process ascendens of the quadrate and the otic capsule. According to von Plessin and Rabinowicz these rami are different in cerebral origin in *Sal. maculata,* but in my section some of the fibres which compose each are easily traced to a common origin. Of the distribution of these nerves nothing need here be said.

The two ophthalmici leave the cranial cavity through the foramen below the process ascendens of the quadrate. The ophthalmicus profundus passes beneath the optic and oculomotorius and breaks up into fibres at the posterior wall of the nasal capsule. Fibres from the ganglion of the seventh are traced through the gasserian ganglion into the ophthalmicus superficialis.

The compound facialis-auditory ganglion is long and narrow. From it arises the palatine branch which goes through

[5]According to these authors the Gasserian ganglion consists of two distinct and separate ganglia: a ventral principal ganglion and a more dorsal accessory portion. The chief ganglion has its proper medullary root, while the root of the accessory ganglion is close by and a little dorsal to the root of the acustico-facialis. From the principal ganglion arise two nerves, called respectively mandibularis (= maxillaris inferior) and nasalis (= ophthalmicus profundus); from the accessory ganglion arise the supramaxillaris superior (= maxillaris superior) and the frontalis (= ophthalmicus superficialis).

the floor of the otic capsule to be distributed as usual. The facialis branch divides into two portions just outside the cranial wall and behind and below the quadrate; the very large posterior branch runs backward to innervate the posterior belly of the digastric muscle. The anterior ramus has the usual distribution.

An especially noticeable feature in connection with the twelfth nerve is the persistence of the dorsal ganglion. Waldschmidt's observations on Protopterus and those of von Plessin and Rabinowicz upon Salamandra are interesting in this connection.

The nasal organ has a well developed organ of Jacobson, though on a simpler type than that of the Cæcilians. The sensory epithelium of the nose, is in these embryos, not differentiated as in the adult.

Conclusions.—Following such students of the Batrachia as Cope and the Sarasins it is with some diffidence that I dissent from their conclusions, for both regard Amphiuma as a connecting link between the Cæcilians and the Urodeles. That both Gymnophiona and Amphiuma are degenerate goes without question, but it seems to me that their many peculiar resemblances are those of homoplassy rather than derivations from a common ancestor. Then again, some of these resemblances have been founded upon mistakes. Thus the possession of an ethmoid by Amphiuma cannot be maintained. The external gills of the larvæ are not so similar as has been supposed; the derotrematous condition which appears later has one important difference: In Amphiuma only the third gill slit persists to open through the round external opening to the exterior, and my material shows that when the other slits were open they had separate openings upon the side of the neck. In Ichthyophis, on the other hand, the observations of the Sarasins show that both the second and third slits have a common external opening.

On the other hand, there are certain differences to be emphasized. The presence of an ethmoid in the Gymnophiona (and its absence from Amphiuma and other Urodeles[6]) the exist-

[6]The ethmoid of H. H. Wilder in Siren is clearly not homologous with the bone (mesethmoid) called by that name in other vertebrates. It is rather the prefrontal of authors.

ence of a turbinal, the absence of a parasphenoid and the presence of a basisphenoid are all points of importance, as is also the frequent presence of two rows of teeth. Again, in the Cæcilians we find a multiplicity of bones such as occurs in the lower Ichthyopsida but not in the Urodeles, and which consequently cannot be derived from the latter. Regarding the chondrocranium of the Gymnophiona no comparison can be made until the appearance of the promised paper by Burckhardt.

The view is quite common that the origin of the Batrachia (sens. lat.) must be sought in the Dipnoi. Thus Cope says (Am. Nat., xviii, p. 725–6, 1884): "The Batrachia have originated from the sub-class of fishes, the Dipnoi, though not from any known form."

This view had doubtless its foundation in the existence of both gills and lungs in these forms. As yet, however, no careful study of the distribution of the cranial nerves and of the ontogeny of the chondrocranium of any Dipnoan has been published, and until we have more detailed accounts than have as yet been made it is safe to assume that the resemblances which have been pointed out between the Dipnoi and the Urodeles are those derived from a common ancestry. Of these resemblances probably the most important is that of the relation of the mandibular arch to the skull. Thus Huxley has divided the Ichthyopsida into autostylic, hypostylic and amphistylic groups, and has shown the close resemblances of the Amphibia to the Dipnoi, Chimæroids and Marsipobranchs in the ampistylic character of this connection of the quadrate with the cranium. It is, however, to be noticed that in the Urodeles the pterygoid cartilage never has that close relation to the cranium that this thesis demands, while the autostylic condition arises comparatively late in development, and never attains that completeness which a Dipnoan ancestry would imply.

In short, I would prefer to trace the origin of both Dipnoi and Urodeles from a crossopterygian ganoid ancestry, the former being the apex of their line of development, the latter tracing their descent through the Stegocephali.

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